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# OCCURRENCE OF ARBUSCULAR MYCORRHIZAL FUNGI IN A PHOSPHORUS-POOR WETLAND AND MYCORRHIZAL RESPONSE TO PHOSPHORUS FERTILIZATION[1]

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The presence of arbuscular mycorrhizas in fens has received little attention, but because fen plants are often phosphorus limited, the plant–fungus interaction could be an important factor in plant competition for phosphorus. In this field study, we determined mycorrhizal colonization rates for 18 fen plant species. Also in the field, we examined the effect of four different forms of phosphorus on the percentage colonization for one fen plant species, *Solidago patula.* We found that in a species-rich, phosphorus-poor wetland both mycorrhizal and nonmycorrhizal species were common. Nine of ten dicotyledonous species examined formed arbuscular mycorrhizas, while all monocotyledonous species were at most very weakly mycorrhizal. A morphological explanation for this pattern is that the monocots in our study have more extensive aerenchyma, especially in coarse roots. Therefore, monocots are able to transport oxygen to their roots more effectively than dicots. In the organic wetland soil, additional oxygen in the rhizosphere promotes phosphorus mineralization and availability. Two of the monocot species (*Typha latifolia* and *Carex lasiocarpa*), which have been described previously as mycorrhizal in other wetland types, are surprisingly nonmycorrhizal in our phosphorus-poor study site, suggesting that a mycorrhizal association would not offer improved phosphorus nutrition to these species. In contrast, our field phosphorus addition decreased mycorrhizal colonization in *S. patula*, suggesting that one benefit to *S. patula* of the mycorrhizas is phosphorus uptake.

**Key words:** aerenchyma; arbuscular mycorrhizal fungi; fen; fertilization; phosphorus; *Solidago patula*; wetland.

The presence of arbuscular mycorrhizal (AM) fungi in wetland plants has received increased attention in recent years (Cooke and Lefor, 1998; Turner and Friese, 1998; Thormann, Currah, and Bayley, 1999; Turner et al., 2000), but uncertainty remains about why some plant species form mycorrhizas while other species do not (Fitter and Merryweather, 1992). The primary abiotic factors known to influence the abundance and distribution of AM fungi are water, nutrient, and oxygen availability (Read, 1991). With regard to these conditions, wetlands comprise a diverse group of systems. It seems likely, therefore, that the costs, benefits, and the importance of mycorrhizas will vary among different wetland types. There is some evidence that plants can regulate the amount of carbon invested in the mycorrhizal symbiosis (Fitter and Merryweather, 1992), suggesting that the controls on the abundance and distribution of AM fungi may depend on how much a plant benefits from the interaction. Because of the uncertain extrapolation of greenhouse results to ecosystems and the difficulty of field manipulations, the ecological implications of the plant–fungus interaction presently are not well understood across different types of wetlands.

For many years there were thought to be clear, family-level distinctions among groups of mycorrhizal and nonmycorrhizal species. Mycotrophy is the ancestral condition in vascular plants (Simon et al., 1993), and until recently the Cyperaceae and Juncaceae, dominant families in many wetlands, were thought to be secondarily nonmycorrhizal (Powell, 1975). However, recent studies have shown the presence of AM fungi (arbuscules and vesicles) in those families, indicating that the phylogenetic patterns are not as clear as they were once thought to be (Wetzel and van der Valk, 1996; Cooke and Lefor, 1998; Miller et al., 1999). Miller et al. (1999) found three classes of species within the genus *Carex*: species that are consistently mycorrhizal, those that are always nonmycorrhizal, and a third group that varies in mycorrhizal status across habitats, apparently in response to local environmental conditions. Mycorrhizal status also varies across habitats in the Typhaceae. *Typha* spp. (cattail) in different habitats have alternately been described as mycorrhizal and nonmycorrhizal (Stenlund and Charvat, 1994; Thormann, Currah, and Bayley, 1999).

Because AM fungi are obligate aerobes, early studies postulated that anoxic conditions would preclude the survival of AM fungi in sites with a consistently high water table (see Mosee, Stribley, and LeTacon, 1981). More recently mycorrhizas have been found in groundwater-fed wetlands (e.g., Turner and Friese, 1998; Miller and Bever, 1999) and submerged, lacustrine plants (e.g., Clayton and Bagyaraj, 1984), where anoxic conditions are common. Miller and Bever (1999) identified two mechanisms by which AM fungi could survive in anoxic conditions. First, certain species of AM fungi may require less oxygen than previously thought. Second, the fungus could be concentrated near the plant root, obtaining oxygen directly from the root or as oxygen diffuses from the root into the rhizosphere.

Despite the ability of AM fungi to persist in anoxic conditions, flooding often has a significant negative effect on the mycorrhizal colonization in wetland plants. Numerous field studies, involving many wetland species, show a general trend toward a higher percentage colonization (Rickerl, Sancho, and

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TABLE 1. Hydrologic and chemical variables at Belle School Fen, New York, USA.

| Water level relative to the peat surface[a] (cm) | Mineralization rate[b] ($g \cdot m^{-2} \cdot d^{-1}$) | Water chemistry (mg/L) | Other variables |
|---|---|---|---|
| Mean = −1.41 (SE 0.58) | N = 1.2 (SE 4.2 × $10^{-3}$) | Ca = 50.3 (SE 6.81) | Average peat depth = 0.5 m |
| Maximum = 7.96 | P = 0.022 (SE 0.040) | Mg = 10.4 (SE 1.55) | Redox potential[c] = −127.1 mV (SE 21.7) |
| Minimum = −4.79 | | Na = 7.73 (SE 0.442) | PH = 7.18 (SE 0.04) |

[a] Hydrologic variables measured during summer 2000.
[b] Nitrogen and P mineralization measured using resin bags buried for 6 wk during summer 2000.
[c] Measured at a depth of 5 cm during summer 1999.

Ananth, 1994; Stevens and Peterson, 1996) and higher fungal diversity (Miller and Bever, 1999) at the drier end of a moisture gradient, sites that are more likely to experience a summer drawdown. Despite similar levels of phosphorus availability and soil inoculum potential across a moisture gradient, Miller (2000) also found lower colonization in wetter sites for two wetland grass species. The mechanism underlying this pattern is still unclear. Stevens and Peterson (1996) found higher colonization in wetter areas in the field and the reverse pattern in greenhouse experiments.

Many studies have found that the primary benefit to the plant of the mycorrhizal symbiosis is improved phosphorus nutrition (see Fitter and Merryweather, 1992). If phosphorus is abundant and available, then the plant does not need to maintain the symbiosis, and mycorrhizal colonization decreases. In greenhouse studies involving many different plant species, high levels of available phosphorus decreased the frequency of mycorrhizal structures (Anderson and Liberta, 1989; Jasper and Davy, 1993; Bobbink, 1998).

Most of the field studies testing the relationship between phosphorus availability and mycorrhizal colonization suggest that increased phosphorus availability leads to decreased colonization. Wetzel and van der Valk (1996) found that mycorrhizal hyphae were more common in low-phosphorus North Dakota wetlands than high-phosphorus Iowa wetlands. In agricultural systems, phosphorus fertilization led to decreased colonization in mulberry (*Morus alba*) (Katiyar et al., 1995) and had no effect on corn (*Zea mays*) (Kabir et al., 1997). Thingstrup et al. (1998) found that flax (*Linum usitatissimum*) relies on arbuscular mycorrhizas for phosphorus uptake at intermediate but not high levels of soil phosphorus. In sagebrush (*Artemisia tridentata*), local phosphorus fertilization lowered arbuscule formation but did not significantly decrease hyphal colonization (Duke, Jackson, and Caldwell, 1994). However, species response may vary. In a field study on different species of plants grown in pots, phosphorus addition increased, had no effect, or decreased AM colonization depending on the plant species involved (Rillig et al., 1998).

Field experiments that test the effect of phosphorus addition on mycorrhizal colonization in natural ecosystems are rare. In addition, experimental field studies are often performed on a single species in a low-diversity system. As demonstrated by Rillig et al. (1998), dynamics of the plant–fungus interaction can vary dramatically among plant species. It is therefore important to examine the mycorrhizal relationship in different species in diverse, natural systems.

The mycorrhizal symbiosis in rich fens offers the opportunity to elucidate aspects of both environmental and phylogenetic controls on the extent of mycorrhizas. Yet, the prevalence and role of mycorrhizas in these species-rich communities have received little attention (Thormann, Currah, and Bayley, 1999; Turner et al., 2000). Rich fens are alkaline peatlands typically fed by groundwater rich in calcium and magnesium. There is evidence that plants growing in these minerotrophic wetlands are phosphorus-limited (Richardson and Marshall, 1986; Bedford, Walbridge, and Aldous, 1999). Therefore, the increased ability to take up phosphorus via mycorrhizas should be highly advantageous to fen plants. However, the consistently high water table in fens creates anoxic soil conditions that may preclude the survival of AM fungi. In three Alberta fens, Thormann, Currah, and Bayley (1999) found no mycorrhizas present in 11 species of herbaceous plants, 6 of which were sedges. Thormann, Currah, and Bayley (1999) did, however, find AM fungal structures in the roots of woody fen plants. Working in disturbed Ohio fens, Turner et al. (2000) found colonization in 18 of 20 species of herbaceous plants. These results are not consistent with an anoxic exclusion of AM fungi, and they invite further research into the prevalence and role of mycorrhizas in fens.

In our study, we examined the extent of mycorrhizal colonization of plants in a groundwater-fed, low-phosphorus New York fen with characteristic high pH and abundant base cations. We also determined the effect of different types of phosphorus fertilization on the mycorrhizal species *Solidago patula*. We hypothesized that (a) because of the low phosphorus availability, arbuscular mycorrhizas would be common in the fen; (b) *Typha latifolia* would be more strongly mycorrhizal than other plants because of its ability to aerate its rooting system and its high nutrient demand; and (c) phosphorus fertilization would decrease mycorrhizal colonization in *S. patula*.

## MATERIALS AND METHODS

***Study site***—The study site, Belle School Fen, is located in central New York near Ithaca (42° N 76° W) in a 24-ha drainage-divide wetland complex. We studied a 0.5-ha portion of the wetland complex dominated by herbaceous, rich fen plant species. The peat at the site averaged 0.5 m in depth. Shallow groundwater had a high pH, was rich in base cations, and fluctuated little throughout the year (Table 1). Mineralization of nutrients, especially phosphorus, was very low (Table 1).

*Carex* spp., *Thylepteris palustris*, and brown mosses (e.g., *Calliergon giganteum* and *Campillium stellatum*) were the most abundant species in the plant community. *Typha latifolia* was also present but not dominant. Woody species including *Toxicodendron vernix*, *Alnus incana*, and *Salix* spp. were also present but uncommon throughout the fen. The plant community was species rich, with between 14 and 28 species of bryophytes and vascular plants per square meter. Typical fen indicator species (e.g., *Solidago patula*, *Toxicodendron vernix*, and *Carex sterilis*) and plants with a more general distribution (e.g., *Typha latifolia* and *Alnus incana*) occurred in the fen.

In addition to the low P mineralization rate (Table 1), there is evidence from plant tissue nutrient data that the plant community at this site is limited by the availibility of P. As a part of a related study at the same site during summer 1998 we collected all aboveground biomass in five 40 × 40 cm plots. We dried, weighed, and analyzed the plant tissue for nutrient content using a

Carlo Erba C/N Analyzer (ThermoQuest, Milan, Italy) to determine N and an ICP to determine P. The average ratio of plant N to P was 18.38 (SE 2.24). Koerselman and Meuleman (1996) and Verhoeven, Koerselman, and Meuleman (1996) found that sites with a plant N : P $>$ 16 are limited by P.

***Plant collection and mycorrhizal assessment***—Between 19 and 23 July 1999, we sampled roots from five plants from each of the 15 most common herbaceous species and the three most common woody species within the fen. Herbaceous plants were gently extracted from the peat, minimizing fine root loss and site disturbance. The entire root system was then washed and the fine roots removed. Sampling of woody species differed. As it was not feasible to extract small trees, we followed the roots from the trunk to the nearest fine roots, which we then removed. All roots were stored at 2°C in 50% ethanol (Brundrett, Melville, and Peterson, 1994).

Terminal fine roots were thoroughly mixed, and a random sample was selected for clearing of the cell contents and staining. Roots were cleared in 10% KOH in an autoclave (121°C, liquid cycle), acidified in 1% HCl, and stained in cotton blue lactoglycerol again in the autoclave using methods modified from Brundrett, Melville, and Peterson (1994). The length of time required for clearing varied across species from 5 min to several hours. Due to a relatively high concentrations of pigments, roots of woody species and of spore-bearing species required long clearing times and sometimes repeated alternation between 10% KOH and 1% HCl solutions. For each sample, 15 15-mm long root segments were mounted on microscope slides and scored (Brundrett, Melville, and Peterson, 1994). Only aseptate hyphae connected to either an arbuscule or a vesicle were scored as mycorrhizal.

Air-filled root porosity was measured for all 18 plant species in this study. Three replicate root samples from each species were separated into two functional groups: fine roots, presumably involved in the uptake of resources, and coarse roots or rhizomes that potentially transport oxygen to the rooting system. Air-filled root porosity for each class of roots was determined using the pycnometric method as described by Jensen et al. (1969) and tested against microscopic methods by van Noordwik and Brouwer (1988).

***Phosphorus addition experiment***—Using five replicate 1-$m^2$ plots per treatment, we fertilized plots with six treatments. The types of phosphorus added were labile P (equal molar ratios of $NaH_2PO_4$ + $Na_2HPO_4$), Fe-P ($FePO_4$), Ca-P ($CaHPO_4$), and an organic form of phosphorus [β-glycerophosphate, $C_3H_5(OH)PO_4Na_2$]. Five control plots were not manipulated. $NaH_2PO_4$ is considered to be available to plants as well as microbes. $FePO_4$, as well as $CaPO_4$, is thought to regulate phosphorus sorption in soils (Reddy et al., 1995). These two forms require chemical transformation before uptake by plants. Organic phosphorus is the most common form of P in peat soils. The form of organic P that we added is thought to be more labile than most of the P-containing compounds in peat.

While the main objective of this paper was to assess the effect of different types of phosphorus fertilization on mycorrhizal colonization, available nitrogen ($NH_4NO_3$) was added separately and with all of the forms of phosphorus to eliminate any possible nitrogen limitation. Nitrogen was added at 6 $g \cdot m^{-2} \cdot yr^{-1}$ and P at 2 $g \cdot m^{-2} \cdot yr^{-1}$. The N addition rate was based on documented rates of agricultural runoff into another New York fen (Drexler and Bedford, 1996) and was approximately triple the atmospheric deposition rate in the northeastern United States (Morris, 1991). Phosphorus addition rates were greater than background plant-available phosphorus but much less than background total phosphorus. The addition rates fell within the range (1.1–10 $g/m^2$) of other published fertilization studies (Richardson and Marshall, 1986; Walbridge, 1991). Nutrients were added in a single pulse on 20 and 21 May 1999. Soluble forms of nutrients were dissolved in deionized water and sprayed over the plots. Insoluble forms were divided into 20 equal amounts and added in a regular grid to the plot surface. At the time of addition, the water level in Belle School fen was below the surface of the peat preventing loss of the added nutrients through surface flow.

On 14 August 1999, we collected roots from one *Solidago patula* plant in each treatment and control plots. As it was necessary to minimize disturbance to the ongoing fertilization study, we followed the roots from the plant stem to the nearest fine roots, which we then removed. The roots were stored, cleared, stained, and scored using the methods described above.

***Statistical analysis***—Percentage colonization data were arcsine square-root transformed. The data from the phosphorus addition study and the root porosity measurements were then analyzed using a one-way ANOVA (PROC GLM; SAS, 1990). In the phosphorus addition study we tested all the treatments with phosphorus against treatments without phosphorus. We also tested each nutrient addition treatment against the control. The root porosity data were tested for differences between monocot and dicot species. Due to the high number of nonmycorrhizal species, the data from the fen community survey of plant species did not become normal when transformed. Therefore, the Mann-Whitney *U* test (SAS, PROC NPAR1WAY) was used to test for differences in percentage colonization between monocots and dicots (SAS, 1990). Because there were only two nonangiosperms in the data set, those species were excluded from the analysis. We considered $\alpha \leq 0.05$ significant.

## RESULTS

***Mycorrhizal colonization of fen plant species***—Arbuscular mycorrhizal structures were absent or very rare in 8 of 18 species (Table 2). The other ten plant species showed varying degrees of mycorrhizal colonization. The most prominent pattern was that all six species of monocots we examined, including *Typha latifolia*, showed almost no evidence of mycorrhizal colonization. In contrast, nine of ten herbaceous dicots were mycorrhizal, showing colonization that ranged from 5 to 56%. The percentage colonization of monocotyledonous species was significantly lower than the percentage colonization of dicots ($P = 0.005$). Of the three woody plants, *Alnus incana* showed evidence of ectomycorrhizas and nitrogen-fixing root nodules, *Toxicodendron vernix* had solely arbuscular mycorrhizas, and *Salix sericea* showed evidence of both ecto- and arbuscular mycorrhizas. All seven herbaceous dicots were arbuscular mycorrhizal. Of the spore plants, *Equisetum arvense* showed mycorrhizal colonization, while *Thelypteris palustris* did not. Roots from monocotyledonous species showed a significantly higher percentage of air-filled root porosity than the roots of dicots for both fine (Table 2, $P = 0.003$) and coarse roots (Table 2, $P = 0.001$).

***Phosphorus fertilization experiment***—The group of treatments that included a form of phosphorus addition produced root colonization that was significantly less than the group of treatments without a P addition (Fig. 1; $P = 0.004$). The addition of N and labile P led to colonization rates lower than the control ($P = 0.04$). The addition of solely labile P and the N plus β-glycerophosphate produced nonsignificant reductions in colonization relative to the control ($P = 0.07$ and $P = 0.09$, respectively). The N, N plus calcium phosphate, and N plus iron phosphate treatments also did not produce colonization rates that were significantly different from the control.

## DISCUSSION

In our study site, where plant-available phosphorus is limiting to plant growth, both mycorrhizal and nonmycorrhizal species are common. The mycorrhizal status of monocots and dicots in this study differed greatly (Table 2). Ten species of monocots, including the site dominants, were generally nonmycorrhizal. Nine out of ten dicot species were mycorrhizal. Given the open canopy and low-phosphorus status of most fens, competition for belowground resources is presumably intense. Fens in both New York and Alberta (Thormann, Currah,

TABLE 2. Percentage arbuscular mycorrhizal (AM) colonization, the presence (+) / absence (−) of three AM fungal structures, and the percent of air-filled pore space in root tissue for 18 fen plant species.

| Species | Family | Arbuscular mycorrhizal colonization | | | | | Root porosity (%) | |
|---|---|---|---|---|---|---|---|---|
| | | Colonization (%) | (SE) | Vesicles | Arbuscules | Hyphal coils | Fine roots | Coarse roots/ rhizomes |
| **Spore-bearing plants** | | | | | | | | |
| *Equisetum arvense* L. | Equisetaceae | 5.7 | 5.2 | + | − | + | 2.8 | 13.0 |
| *Thelypteris palustris* Schott. | Polypodiaceae | 0 | 0 | − | − | − | 1.4 | 0.8 |
| **Monocots** | | | | | | | | |
| *Carex flava* L. | Cyperaceae | 0 | 0 | − | − | − | 29.5 | 8.6 |
| *C. hystericina* Muhl. | Cyperaceae | 0 | 0 | − | − | − | 23.3 | 10.4 |
| *C. lasiocarpa* Ehrh. | Cyperaceae | 0 | 0 | − | − | − | 4.5 | 21.8 |
| *C. sterilis* Willd. | Cyperaceae | 0.3 | 0.3 | + | − | − | 27.7 | 9.2 |
| *Eleocharis tenuis* (Willd.) Schultes. | Cyperaceae | 0 | 0 | − | − | − | 7.4 | 12.2 |
| *Typha latifolia* L. | Typhaceae | 0 | 0 | − | − | − | 13.5 | 20.6 |
| **Dicots** | | | | | | | | |
| *Alnus incana* (L.) Moench. | Betulaceae | 0 | 0 | − | − | − | 0.9 | 0.8 |
| *Clematis virginiana* L. | Ranunculaceae | 55.5 | 6.1 | + | + | + | 4.8 | 4.3 |
| *Eupatorium maculatum* L. | Asteraceae | 7.7 | 5.2 | + | + | − | 0.7 | 3.5 |
| *Hydrocotyle americana* L. | Apiaceae | 29.1 | 3.1 | + | − | − | 3.1 | 0.6 |
| *Lycopus uniflorus* Michx. | Lamiaceae | 37.7 | 10.0 | + | + | + | 1.5 | 2.3 |
| *Rubus pubescens* Raf. | Rosaceae | 41.4 | 5.5 | + | + | − | 2.9 | 0.7 |
| *Senecio aureus* L. | Asteraceae | 55.5 | 8.2 | + | + | − | 4.0 | 2.5 |
| *Solidago patula* Muhl. | Asteraceae | 35.3 | 10.4 | + | + | + | 2.8 | 1.0 |
| *Salix sericea* Marshall. | Salicaceae | 3.0 | 2.1 | + | − | − | 3.8 | 2.0 |
| *Toxicodendron vernix* (L.) Kuntze. | Anacardiaceae | 32.0 | 6.5 | + | + | − | 6.9 | 1.1 |

and Bayley, 1999) are dominated by nonmycorrhizal species, suggesting that nonmycorrhizal species must have effective alternative strategies to acquire nutrient resources.

Although there are many morphological differences between monocot and dicot roots, one difference in particular, the high proportion of aerenchyma in monocot roots, could potentially explain the pattern in mycorrhizal colonization. Generally, monocots have much higher percentage of air-filled aerenchyma in their roots than dicots (Crawford, 1989). The species examined in this study showed the same pattern (Table 2). In low-nutrient, frequently anoxic soils, plants with extensive aerenchyma have two distinct advantages. First, transport of oxygen through aerenchyma to root tips allows monocots to maintain aerobic respiration in root cells. This mechanism allows plants to support more extensive root systems and potentially exploit a larger soil volume than plants without extensive aerenchyma (Crawford, 1989). Second, oxygen leaking from the root into the rhizosphere can stimulate aerobic decomposition close to the root. Saprobes in the rhizosphere mineralize nutrients that the plant can then acquire (Moore, Lafer, and Funk, 1994). Two studies with rice cultivars have found a negative relationship between available P and per-

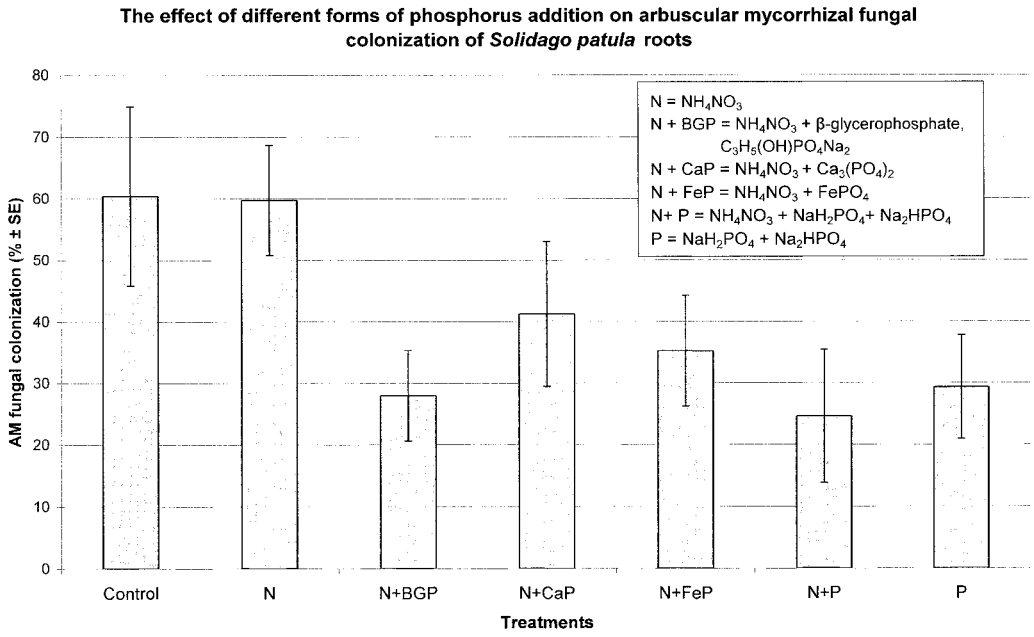


Fig. 1. AM fungi percentage colonization in *Solidago patula* across different nutrient addition treatments. The group of treatments with P added was significantly different than that with no P added ($P = 0.004$).

centage root porosity, suggesting that aerenchyma may play a role in facilitating P uptake (Kirk and Du, 1997; Lu et al., 1999). *Typha latifolia* is known to be especially effective at aerating its roots and rhizosphere (Bedford, Bouldin, and Beliveau, 1991; Bendix, Tornbjerg, and Brix, 1994). Also, we have preliminary data that *T. latifolia,* but not mycorrhizal dicots, responded to the addition of organic P with higher tissue P concentrations, possibly through this mechanism (unpublished data).

***Controls on arbuscular mycorrhizal fungi***—The results of the P fertilization study (Fig. 1) are consistent with the hypothesis that P nutrition is, at least for some plant species, an important benefit of the mycorrhizal symbioses. The negative effect of P on percentage colonization in *Solidago patula* is consistent with the results of numerous greenhouse studies (Anderson and Liberta, 1989; Jasper and Davy, 1993; Bobbink, 1998). There is some debate as to how strongly the plant can control the mycorrhizal symbiosis (Fitter and Merryweather, 1992). However, the fact that this and other studies have found a decrease in colonization in response to elevated P suggests that plants can control, with at least some degree of precision, the extent of mycorrhizal colonization in their roots (Thompson, Robson, and Abbot, 1986; Anderson and Liberta, 1989). Understanding the mechanism associated with this pattern will require further work.

Because of the low nutrient status of fens and the well-established benefits of AM fungi for P uptake, we expected that most fen species would be mycorrhizal and that species with variable mycorrhizal colonization in other studies would be strongly mycorrhizal in fens. These hypotheses proved to be incorrect. Although we found nine dicots to be mycorrhizal, the monocots, which dominate many wetlands including our fen, were nonmycorrhizal. Both *Typha latifolia* and *Carex lasiocarpa,* which were mycorrhizal in other studies (Cooke and Lefor, 1998; Turner et al., 2000), were nonmycorrhizal in this study site. This result is especially surprising for *T. latifolia,* as it has the physiological capability to become much more dominant in our study site. *Typha latifolia*'s lack of dominance is thought to be due to low P availability, a condition that would seem to make a mycorrhizal symbiosis more advantageous (Vaithiyanthan and Richardson, 1999). The absence of AM fungi from the roots of *T. latifolia* and *C. lasiocarpa* at this low-P site suggests that P availability may not be important in determining in which habitats these species form mycorrhizas. In a comprehensive study of mycorrhizas in the genus *Carex,* Miller et al. (1999) predicted a relationship between soil P availability and AM fungal colonization and failed to find a correlation. Their results, like ours, suggest that, among some wetland species, P uptake may not be the sole benefit to the plant of the mycorrhizal symbiosis.

An alternative hypothesis is that the degree of seasonal water stress controls the extent of mycorrhizal colonization for some wetland species. In our groundwater-fed study site, the water level varies little throughout the year (Table 1). However, in other published studies of mycorrhizal colonization in *Typha* spp. and *Carex* spp., the plants were growing in wetlands with much greater seasonal fluctuation in water level, often marshes or prairie potholes (Wetzel and van der Valk, 1996; Cooke and Lefor, 1998; Miller et al., 1999). Mycorrhizas have been shown to benefit many plant species in times of water stress (Fitter, 1988; Davies, Potter, and Linderman, 1999). Consistent with this hypothesis, Rickerl, Sancho, and Ananth (1994), Stevens and Peterson (1996), and Miller (2000) all found that for a number of wetland species mycorrhizal colonization increased toward the drier end of a moisture gradient. Because many other resources and conditions covary with moisture, these studies do not conclusively prove this alternative hypothesis. They do suggest, however, that the benefits of arbuscular mycorrhizas to some wetland species may be realized during seasonal drawdowns.

The contrast between our findings for *Typha latifolia* and *Solidago patula* suggests that the benefits to the plant of AM fungi can differ among plant species. We found that *T. latifolia* was nonmycorrhizal in a phosphorus-poor environment and that *S. patula* responded to phosphorus addition by decreasing mycorrhizal colonization. These findings are consistent with Rillig et al.'s (1998) results. Our study suggests that the benefits of the mycorrhizal association can vary among plant species. These findings support the large and growing body of evidence for the assertion that the mycorrhizal symbiosis in ecosystems is a complex and variable interaction. Understanding the ecological function of AM fungi in a given ecosystem requires field surveys and manipulations in addition to greenhouse studies.

***Ecological implications***—The fen plant community contains dominant nonmycorrhizal monocots and mycorrhizal subdominant dicots. There is evidence that in other systems with dominant nonmycorrhizal plants and subdominant mycorrhizal plants that mycorrhizas can maintain plant species richness by allowing the persistence of some species of plants that would otherwise be out-competed (Grime et al., 1987; Gange, Brown, and Sinclair, 1993). If interspecific competition in fens operates as it does in other systems, then the presence of arbuscular mycorrhizas helps maintain plant species richness in fens.

The difference between hummock and hollow soil environments may play an important role in the prevalence of mycorrhizas in fens. Many, though not all, of the dicot species sampled in this study were more common on hummocks than in hollows. At the site, clonal monocots formed a matrix throughout the fen, becoming especially dominant in the hollows. Examining roots in one species, white cedar (*Chamaecyparis thyoides*), Canelmo and Ehrenfeld (1999) found more AM fungal colonization in hummock roots than in hollow roots. Though more work needs to be done, our results suggest that this pattern may hold across species, with mycorrhizal species located more often on hummocks and nonmycorrhizal species more often growing in hollows.

The results of our study suggest that mycorrhizas are present and important in fens. The interaction between water and nutrient availability could be important in determining the extent of the mycorrhizal symbiosis among some species of wetland plants. Variation in mycorrhizal colonization among different species of wetland plants and the role of AM fungi in competition for P could be very important in structuring fen plant communities. Mycorrhizas may also play a role in the maintenance of the high species richness in fens, perhaps by allowing the persistence of some subdominant dicot species.

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